

DESCRIPTION AND BIOLOGICAL INTERPRETATION OF SOME VICTORIAN TRILOBITE HYPOSTOMES

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Summary

Some Lower Devonian trilobite hypostomes are described, and functions suggested for the various structures. The trilobite hypostome is interpreted as an originally dorsal axial structure which has become ventral through mouth migration, and fulfilling the functions of protection for the proventriculum, protection for the mouth in some forms, support for the head in some forms, a base for the antennae, and attachment for cephalic muscles. The function of the maculae is discussed.

Introduction

The trilobite mouth was not at the anterior extremity of the animal, but a ventral structure set well back near the posterior margin of the cephalon. The mouth was an orifice situated between two hard plates, the anterior one being the hypostome and the posterior one being the metastome. These were hard plates like those of the dorsal surface, and not a relatively soft integument such as was characteristic of the ventral surface of trilobites. The soft integument is reminiscent of that of the annelids from which no doubt the trilobites sprang.

It is generally agreed that the hypostome of the trilobite is homologous with the labrum of other arthropods, but from what somite it developed it is very difficult to say, because hypostomes are only known in late larval and adult stages of trilobite life history. Much remains to be discovered concerning cephalization in the trilobites, but Störmer's (1942) review of existing knowledge suggests that the hypostome belongs to the pre-antennal segment.

Mouth Migration

Primitively, the mouth is a terminal anterior structure. In annelids it is almost so, there being a single pre-oral segment, the prostomium. In trilobites, there has been mouth migration whereby the mouth has receded to a position at the back of the cephalon on the ventral side.

One of the main differences between the trilobite families Homalotidae and Calymenidae is that the epistome is on the dorsal surface of the former but on the ventral surface of the latter. This may well be another expression of the process of migration which involves the mouth.

Axis and Hypostome

The three-fold longitudinal division of the trilobite carapace which gives it its name is not just a superficial structure of small biological moment. The axis appears first in ontogeny. That is, the longitudinal

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divisions appear before the transverse segmental divisions, e.g. see Brögger's larval series of *Liostracus*. The axis may thus deserve more attention in ontological interpretations than it has received. In such a study, the hypostome should find a place, because—

1. It is an axial structure, corresponding in position on the ventral surface with the better known axial structures on the dorsal surface.

2. It approximates in shape to the glabella (the dorsal axial structure of the cephalon), and has no relation to the shape of the cephalon.

3. The hypostome (in the cases studied by me at any rate) has the same ornament as that on the glabella. For instance, the hypostome of *Lichas* has tubercles on it like those on the glabella, that of *Phacops* possesses the coarse granulation such as appears on its glabella, and the very fine granulation of the dorsal shield of *Odontochile* is found likewise on the hypostome. This is in contrast with the ventral integument, which was smooth except for strengthening rings. It had no ornament comparable with that of the dorsal surface.

4. The hypostome and metastome were comparatively thick and hard plates such as found on the dorsal surface and nowhere else on the ventral surface. The ventral integument was very thin.

5. The hypostome is generally inflated to a degree comparable with the glabella in each case, and in the same relative direction. If there were no mouth migration, the hypostome would appear on the dorsal surface, a plate similar in size, shape, ornament and inflation to the glabella.

6. The hypostome forms a continuity with the dorsal axial plates, being attached by the hypostomal suture to the reflexed margin of the cephalic shield. In the Olenellidae and some other Cambrian forms there is not even a hypostomal suture present (Störmer, 1942, p. 133).

On this interpretation, the hypostome is regarded as a part of the axial section of the dorsal shield reflexed to the ventral surface as a result of mouth migration. But whereas the glabella represents a number of segments, the hypostome probably represents only one or part of one segment (cf. Störmer, 1942, p. 123). Some of the similarities between the glabella and hypostome listed above are no doubt due to the fact that the hypostome is adapted as a ventral plate corresponding to the dorsal glabella. The two plates apparently protected a large proventriculum. However, there is ample evidence, in my view, that the hypostome is essentially a part of the dorsal axial shield which has been reflexed to the ventral surface, and is not primarily a ventral structure.

Biological Significance of Hypostome

More must be known about the hypostomes of various genera and species and their relation to the rest of the cephalon before adequate interpretations of their biological significance can be made. Sections showing the relations of the wings, alae, and furrows of the hypostome to the muscular apodemes of the glabella would be a big help. However, the following appear to be among the functions of the hypostome:

1. *Protection for Proventriculum.* A number of writers have suggested that the space between the convex glabella and convex hypostome

was occupied by a proventriculum, e.g. Raymond 1920, Richter 1925. Judging by analogy, this is very likely. If this were so, then clearly one function of the hypostome would be that of support and protection for the proventriculum.

Raymond (1920, p. 81) suggested that the strong development of the frontal lobe of the larvae was due to their changing over from a pelagic to a more benthonic habit as they came to maturity. This change would make necessary a larger stomach because the benthonic animals were apparently omnivorous and some of them mud-eaters, in contrast with the pelagic larvae which ingested more or less pure protein in the form of microzoa. One would expect to find some similar difference between the pelagic and the benthonic adult trilobites, and this would be reflected in the amount of space between the glabella and the hypostome. The pelagic forms generally have small hypostomes, even if bulbous, but some of them are relatively flat. The glabella is usually small, too. There does appear to be a difference in the size of the proventriculum (so inferred) between pelagic and benthonic trilobites, but such differences should be calculated with reference to relative body weight. The pelagic forms were of lighter construction, and there would therefore be less physiological upkeep.

2. *Protection for Mouth.* The presence of a convex hypostome meant that the mouth was recessed and so protected. This would be an advantage, one imagines, particularly in the mud-burrowing forms, some of which strongly forced their way through sediments, digging deep trails which have been preserved (Walcott, 1924, pp. 124-125).

It would appear that in some cases at any rate the hypostome overlapped the mouth to a small extent, and that the metastome overlapped the bases of the cephalic appendages (see Störmer, 1939, fig. 26). This overlapping of structures would give a streamlined effect when the animal was moving forward. It has been suggested to me that this arrangement could have been for closing the mouth, a necessary function if the food or food-bearing mud were drawn into the proventriculum, then forced along the alimentary canal.

3. *Support for Head.* The thorax and pygidium of the trilobite were provided with segmentally arranged perambulatory appendages, but the cephalic appendages were set behind the metastome, i.e., at the very back of the cephalon (Störmer, 1939, fig. 26; Walcott, 1924, pl. 30, figs. 17, 18), and were smaller in size and apparently differed somewhat in function. The head with its large proventriculum and long antennae was probably the heaviest part of the animal per unit length, and yet it did not have the support from ambulatory appendages provided for the rest of the body. It may be that the convex hypostome aided (in the case of the benthonic forms) by constituting, if needed, a kind of skid which could rest on the bottom while food or food-bearing mud was fed into the mouth.

4. *Base for Antennae.* The tactile antennae of trilobites arose bisymmetrically from the lateral margins of the hypostome on the ventral surface. In specimens showing the antennae *in situ*, they are contiguous

with the hypostome, and indeed may have been continuous with it. The hypostome thus afforded them a measure of stability. The antennae emerge from the posterior margins of the anterior wings. Here the hypostome is strongest, being broadest, and being buttressed with wings in the horizontal plane, and often also with alae in the vertical plane.*

In the hypostome of *Odontochile formosa* described in this paper, there are well-defined recesses behind the anterior wings. The anterior and marginal furrows converge on these points, and if the furrows are associated with the muscular system (as suggested in a later paragraph), then this convergence may indicate an important centre of muscle attachment associated with the antennae. In the phacopid hypostomes described in this paper, there are also recesses, and from them dorsally directed alae are placed so as to constitute a continuation of the recess walls. And the alae are not flat, but rounded in such a way as to suggest that they were moulded to the shape of the antennae. However, it is not meant to suggest that the hypostome and antennae therefore belonged to the same larval segment.

5. *Attachment for Muscles.* The wings and alae of the hypostomes constituted biologically valuable apodemes for the attachment of muscles (see Öpik 1937, Whittington 1941). They provided a large surface area for this purpose, and angles of operation different from those of the main body of the hypostome. In this connection the alae may be compared with the appendifers of the dorsal shield, with which possibly they may prove to be homologous. It is considered likely that the furrows of the hypostome were also of the nature of apodemes to facilitate the attachment and operation of cephalic muscles. They may be compared with the furrows and ridges of the pygidial and thoracic pleurae, and of the cephalon.

6. *Function of Maculae.* There has been considerable argument as to the function of the hypostomal structures called maculae. Three theories have been advanced:

- (a) that they are visual organs (Lindström).
- (b) that they are 'glandular intumescences' (Novak).
- (c) that they are organs for muscle attachment (Barrande).

(a) If the structures are visual organs, then they must be organs of the ventral surface of the hypostome, and in a position where they will receive light. Only so would they be capable of functioning. As far as I have been able to ascertain, the structures concerned affect the whole thickness of the hypostomal plate (cf. Lindström, 1901, p. 8). With regard to position, the maculae are on the posterior half of the hypostome, and in the case of those with tumid hypostomes they are in the shadow of the tumid part. This seems a very unlikely location for visual organs.

A priori, it may be considered that hypostomes may or may not have maculae interpretable as visual organs, just as there are trilobites with and without dorsal eyes, but nevertheless, just as pelagic trilobites have

*In this paper the term 'wings' is employed for horizontal extensions of the margin of hypostomes, and the term 'alae' is used for dorsal extensions. There appears to be value in thus distinguishing these two types of processes.

more pronounced eyes than benthonic trilobites, so it would be anticipated that pelagic forms would have well-developed maculae (if they are visual organs) and benthonic forms poorly developed maculae or none at all. Swimming in the clear water, the pelagic trilobites could benefit from ventral vision in addition to the dorsal and lateral vision afforded by the dorsal eyes. The benthonic trilobites, on the other hand, crawling along the bottom or digging in the mud of the sea-floor, would have little opportunity (if any) of using ventral visual organs. In matter of fact, maculae are rare in the pelagic forms (like the Lichadids and Acidaspids), but the benthonic forms (like the Asaphids, Proetids, Scutellids, Dalmanitids, and Homalonotids) frequently have well-developed structures.

Furthermore, if the maculae are visual organs, it will be anticipated that any curved surfaces thereof will be convex on the ventral side, i.e., so as to assist vision and not interfere with it. Actually, in a great number of maculae (as in *Odontochile formosa*, for instance) the surfaces are indented, being concave on the ventral surface. It is difficult to interpret such structures as visual organs.

Parts of the surfaces of a few maculae are granulated in such a way as to simulate the lenses of dorsal eyes (Lindström, 1901). This is the best evidence Lindström had for his argument that the maculae are visual organs. Nevertheless, if they are lenses, it would naturally be anticipated that they would cover the whole macular surface and not just part of it. These structures are not really understood yet, and at present are capable of other interpretations.

(b) That the maculae are 'glandular intumescences' (drüsenartige Anschwellungen) is just a guess, with no supporting evidence apart from the tumidity of the maculae. The theory does not account for the specialized structures described by Lindström, nor for the fact that some maculae are in the form of depressions and not intumescences.

(c) If the maculae are organs of muscle attachment, then they must be organs of the dorsal surface of the hypostome. Such an interpretation must give a satisfactory interpretation of the position and the specialized structures of the maculae—the convex and concave surfaces, and the protuberances called lenses by Lindström. To interpret these structures in terms of such a function can be done, but whether it is correct or not is another matter. Fields of muscle attachment are sometimes raised and sometimes excavated. The maculae, whether convex or concave, could therefore on their dorsal side be structures with muscle attachment function. The 'lenses' of Lindström were small hollows on the dorsal side of the hypostome, and could likewise possibly fulfil a function of muscle attachment.

The writer's opinion is that no fully satisfactory explanation for all maculae has yet been offered, but of the three discussed above, that interpreting them as muscle attachments has so far least to disfavor it. The great variety in structures of the maculae may well indicate some variation in type of function, so that no one interpretation is adequate for all. Barrande (1852) figured a Dalmanitid hypostome with four maculae (Pl. 25, fig. 20).

Hypostome of *Odontochile formosa*

Pl. XIV, fig. 8.

Specimen Described. Nat. Mus. Vic. Reg. No. 14597, preserved in bluish-grey shale from Carmen's Quarry, in the valley of Scrubby Creek about $1\frac{1}{2}$ miles south of Kinglake West Post Office. Grid reference of locality on Kinglake Military Map (1930 edition): 249758. Hypotype.

Description. Sub-quadrate in outline, broader anteriorly than posteriorly. Length (median longitudinal axis), 21 mm.; greatest width, i.e., across anterior end, 23 mm.; and width across middle, 19 mm. Anterior margin slightly curved, and terminating laterally in small wings which extend horizontally only 2.5 mm. beyond the lateral margins of the hypostome. A faint furrow follows the anterior margin, and then near the wings curves back to meet the lateral furrows at the posterior margins of the wings. Posterior margin well rounded and denticulate. One denticle is evident at the posterior extremity of the hypostome, and there is also trace of one to the left of it as one looks at the specimen, i.e., on the right-hand side of the animal. A shallow marginal furrow occurs at the posterior end, and is limited to that end.

A comparatively deep furrow occurs 4 mm. from the posterior end; on reaching the lateral margins this furrow continues along them as far as the anterior lateral wings. The ends of the furrow turn out towards the posterior margins of the wings, and they coalesce with the ends of the anterior marginal furrow.

Approximately half way down the length of the hypostome a macula is present on each side of the midline, and between it and the lateral furrows. A furrow connects the maculae. As figured, the hypostome is viewed from the ventral surface, and the maculae show as deep impressions; these would show as strongly raised areas on the dorsal surface. As the specimen has suffered slight compression, the precise amount of tumidity it originally possessed is not known, but it is clear that it was not great.

Traces of the original ornament are preserved on the specimen. It can be readily seen in the short posterior marginal furrow, and consists of a fine granulation as seen on the dorsal shield of *Odontochile formosa* (Gill, 1948).

Comment. Although not found in place in a specimen of *O. formosa*, the hypostome presumably belonged to that species because—

- (a) in size and proportions it would fit well the cephalon of that species;
- (b) it possesses the same kind of surface ornament;
- (c) it occurs in beds where this trilobite is plentiful, but no other has been collected to my knowledge.

The hypostome of *O. formosa* contrasts with that of *Dalmanites wandongensis*, figured by McCoy (1876, Pl. XXII, fig. 3), further emphasizing the difference between these forms which until recently were both described as *Dalmanites meridianus* (Gill, 1948).

Phacops sp. Hypostome in situ

Pl. XIV, figs. 1-2.

Specimen Described. Steinkern of cephalon and thorax of trilobite in light greyish brown shale from Syme's Homestead, Killara, Victoria (for exact locality see map in Gill, 1945). Nat. Mus. Vic. Reg. No. 14598.

Description. This trilobite is an example of a species which has been known locally as *Phacops fecundus* Barrande, but is not really such, although of that type. The cephalon is at right angles to the thorax, and the glabella has been broken away, revealing the hypostome *in situ*. It is moderately tumid, the convex surface being ventral. The anterior border is broken away but enough is preserved to show that anterior wings were present. The posterior end of the hypostome is narrower than the anterior end, and the posterior margin is well rounded. There is a clearly defined but shallow posterior marginal furrow. The hypostome on this specimen extends as far back as the posterior margin of the glabella, i.e., to the nuchal furrow. Begg (1943) described some hypostomes *in situ* and also noted their extension to almost the back of the cephalon. This means that the mouth, metastome, and cephalic appendages were all accommodated in a very short space; the cephalic appendages must therefore have been small (cf. Raymond, 1920, fig. 13).

Hypostomes of Some Phacopid Trilobites

(1) The first specimen of this group (Pl. XIV, figs. 3, 4) is the steinkern of a phacopid hypostome in brownish-grey sandy shale from Syme's Quarry, Killara, Victoria (for precise locality see map in Gill, 1945). Nat. Mus. Vic. Reg. No. 14599.

The hypostome is 19 mm. long (midline) and 17 mm. wide across the alae (greatest width). The posterior margin is incomplete, but the width there was about 12 mm. These measurements are taken in a flat plane and not following the curvature of the hypostome. The median longitudinal profile rises about 4.5 mm. above the line joining the anterior and posterior margins. Not only is the lobe of the hypostome tumid, but also the posterior and lateral furrows are deep.

There is also a very narrow but well-defined anterior furrow, which the frontal lobe overhangs. The great tumidity of this hypostome has obscured the frontal furrow and almost obliterated the middle furrow, as this is represented only by a change in contour without any trough being present.

The surface is covered with strong pustules of varying sizes which affect the whole thickness of the hypostome, i.e., the ornament appears on both steinkern and external mould.

(2) The second specimen of this group (Pl. XIV, figs. 6, 7) is the steinkern of a hypostome in light greyish-brown shale from Syme's Homestead, Killara, Victoria. Nat. Mus. Vic. Reg. No. 14600.

This hypostome is similar to (1) but is readily distinguished by the clear development of the middle furrow, and the presence of a fine instead of a coarse 'ornament'.

(3) The third specimen of this group (Pl. XIV, fig. 9) is also a steinkern in light brownish shale from Syme's Homestead, Killara, Victoria. Nat. Mus. Vic. Reg. No. 14601.

Length (midline)	9.5 mm.
Width across alae	9 mm.
Width at posterior end	4 mm.

It is like hypostome (2) in having a well-defined middle furrow, and possessing a fine ornament. The hypostome may be from an early moult of the same species, its small size thus being accounted for.

Hypostome of an *Odontopleurid* Trilobite

Pl. XIV, fig. 5.

This specimen is a steinkern in light greyish-brown shale from Syme's Homestead, Killara, Victoria. Nat. Mus. Vic. Reg. No. 14602.

Length (midline)	4 mm.
Width across alae	5 mm.
Width near posterior end	3.5 mm.

Hypostome quadrate, with slightly arched anterior and posterior borders. Moderately tumid, the lobe rising about 1 mm. above the plane of the margins. Alae on anterior wings. A marginal furrow follows the lateral and posterior borders, terminating in shallow pits beside the wings. Furrows extend from these pits a short distance on to the central lobe. Barrande (1852, Pl. 39, fig. 40) has figured similar furrows on '*Acidaspis prevosti*', and somewhat similar furrows appear in *Lichas* (Begg, 1943, Pl. II, fig. 6).

The pits on this hypostome are proportionately larger and shallower, and also in a different position from typical maculae, so are probably not homologous with them.

Odontopleura spp. have been recorded from Killara (Gill, 1938, p. 170), but the specimens stand in need of re-study.

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Description of Plate

PLATE XIV

All figures $\times 2$.

- Figs. 1-2.—*Phacops* sp. Hypostome *in situ*. Note also anterior doublure of cephalon, axial furrow, and eyes.
- Figs. 3-4.—Hypostome of phacopid trilobite. In fig. 3 the specimen is turned to one side to show ala extended dorsally at right angles to the main body of the hypostome.
- Fig. 5.—Hypostome of odontopleurid trilobite.
- Figs. 6-7.—Hypostome of another phacopid trilobite. The figure on the left shows the specimen turned to one side to display the ala.
- Fig. 8.—Hypostome of *Odontochile formosa* Gill.
- Fig. 9.—Small hypostome of phacopid trilobite.